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REVIEW

Efficacy and ethics of intensive predator management to save endangered caribou

Chris J. Johnson[1] | **Justina C. Ray**[2] | **Martin-Hugues St-Laurent**[3]

[1]Ecosystem Science and Management, University of Northern British Columbia, Prince George, British Columbia, Canada

[2]Wildlife Conservation Society Canada, Toronto, Ontario, Canada

[3]Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, Centre for Forest Research, Centre for Northern Studies, Rimouski, Québec, Canada

Correspondence
Chris J. Johnson, Ecosystem Science and Management, University of Northern British Columbia, BC, Canada.
Email: johnsoch@unbc.ca

Abstract

Lethal population control has a history of application to wildlife management and conservation. There is debate about the efficacy of the practice, but more controversial is the ethical justification and methods of killing one species in favor of another. This is the situation facing the conservation of woodland caribou (*Rangifer tarandus caribou*) in Canada. Across multiple jurisdictions, large numbers of wolves (*Canis lupus*), and to a lesser extent bears (*Ursus americanus*) and coyotes (*C. latrans*), are killed through trapping, poisoning or aerial shooting to halt or reverse continued declines of woodland caribou. While there is evidence to support the effectiveness of predator management as a stop-gap solution, questions remain about the extent to which this activity can make a meaningful contribution to long-term recovery. Also, there are myriad ethical objections to the lethal removal of predators, even if that activity is in the name of conservation. Debates about predator management, just one of numerous invasive actions for maintaining caribou, are made even more complex by the conflation of ethics and efficacy. Ultimately, long-term solutions for the recovery of caribou require governments to stop delaying difficult decisions that address the real causes of population decline, habitat change.

KEYWORDS

anthropogenic disturbance, compassionate conservation, conservation strategy effectiveness, ethics, gray wolf, management tool, predator management, public support, *Rangifer tarandus caribou*, woodland caribou

1 | INTRODUCTION

Often the most challenging conservation problems are those that involve multiple threats that act in combination, particularly in the last stages of population loss or species extinction (Brook et al., 2008). That amalgam can be compounding, interactive or synergistic, and is especially complex when human activities alter natural community dynamics to the disadvantage of a species of conservation concern. Anthropogenic activities, for example, can directly reduce the availability or quality of habitat, and those changes then influence the competition or predator–prey dynamics between two or more species (DeCesare et al., 2010). Lethal or nonlethal population control is one possible intervention when one of those species is at peril of extinction and an interspecific

interaction, even if human mediated, is the most immediate cause of decline.

Population control is not an uncommon conservation strategy, especially in the context of invasive species (Hampton et al., 2019; Russell et al., 2016). The notion of eradicating any species can be unpalatable, but for species introduced into places outside their natural range, such activities are commonly justified through their benefits to the functioning of an ecological community, the persistence of an endangered species or advancement of human interests (Crowley et al., 2017; Prior et al., 2018; Simberloff et al., 2013). In North America, for example, we enact programs that result in the removal of introduced American bullfrog (*Lithobates catesbeianus*) or bighead carp (*Hypophthalmichthys* spp.) to the benefit of aquatic ecosystems (Cupp et al., 2017; Govindarajulu et al., 2005). The poisoning and trapping of a suite of invasive mammalian predators are common practice in New Zealand and deemed necessary to maintain the native flora and fauna, many of which are endangered (Russell et al., 2016).

The community dynamics of interacting species can be difficult to unravel and the preference for one species over another, even if that species is endangered, can be challenging to argue. Barred owls (*Strix varia*), for example, are expanding their range across southwestern Canada and northwestern USA and are displacing the less competitive, but endangered northern spotted owl (*Strix occidentalis caurina*). An effective, but controversial conservation action is the lethal removal of this colonizing species, which has led to local population recovery of spotted owls (Diller et al., 2016). The endangered Channel Island fox (*Urocyon littoralis*) was threatened by a set of complex community interactions including predation by the protected golden eagle (*Aquila chrysaetos*). The prevalence of feral pigs (*Sus scrofa*) allowed the eagle to maintain a constant population even as the endemic fox, the native prey, declined in abundance (Roemer et al., 2001). In that case, pigs were eradicated, golden eagles were relocated to the mainland, and marine-dependent bald eagles (*Haliaeetus leucocephalus*) were introduced to fill the niche formally occupied by the golden eagle. The "apparent competition" (Holt, 1977, 1984) between foxes and pigs is in fact a predator–prey dynamic that is well documented in other systems, often with implications for conservation and management (DeCesare et al., 2010; Rominger, 2018). In such cases, the most obvious solution is to remove the primary prey species or the predator to the advantage of the endangered species.

Across much of Canada, and formerly portions of the United States, many populations of woodland caribou (*Rangifer tarandus caribou*) have disappeared or are facing extirpation (COSEWIC, 2014a, 2014b). Woodland caribou are a relatively low-density, sedentary subspecies of *Rangifer* that were formally found across the majority of boreal and sub-boreal forests and mountains of Canada and the contiguous United States. Caribou have demonstrated considerable range contraction and population decline across much of their distribution in Canada, and they were recently extirpated from the mountains of northern Idaho (Courtois et al., 2003; Hervieux et al., 2013; Johnson et al., 2015; Santomauro et al., 2012; Schaefer, 2003). Of the 54 populations in British Columbia, 14 have fewer than 25 individuals (Government of BC, 2018). Population declines are the result of a suite of threats including direct habitat loss and displacement by human activities (Seip et al., 2007). However, a large body of evidence points to human-mediated apparent competition as the most likely direct cause of decline and extirpation for many populations of caribou (Frenette et al., 2020; Wittmer et al., 2005). Following from this complex set of community interactions, caribou suffer from unsustainable predation from canids (e.g., gray wolves *Canis lupus*) and felids (e.g., cougar *Puma concolor*). Those predators are supported by abundant populations of moose (*Alces americanus*) or other deer species (*Odocoileus* spp.) that benefit from an increase in the availability of forage associated with younger forests (Serrouya et al., 2011). Anthropogenic disturbance, such as forestry or oil and gas activities, also produce roads and other linear features that allow both the predators and their prey to access larger portions of caribou range (Blagdon & Johnson, 2021; Mumma et al., 2018). In the past, predator populations were regulated by the dynamics of their primary prey, caribou. Now, more fecund moose and deer support increasing populations of predators to the detriment of the relatively low-productivity caribou (Bergerud et al., 2008; Ozoga, 1987; Sæther & Haagenrud, 1983).

Although the ultimate cause of caribou decline is human-mediated landscape disturbance, restoration of habitat, both suitable for caribou and disadvantageous to moose and deer, will take decades to accomplish (Lacerte et al., 2021; Ray et al., 2015). Those efforts are complicated by climate-driven increases in wildfire and concurrent losses of habitat as well as related changes in the density and distribution of apparent competitors such as deer (Barber et al., 2018; Dawe & Boutin, 2016). Despite over 15 years of intended protection under the federal Species at Risk Act, many populations of caribou in Canada continue to be subjected to increasing levels of habitat clearing and other human activities that degrades the availability or quality of habitat (Nagy-Reis et al., 2021; Rudolph et al., 2017). The failure to fully address the underlying mechanisms of decline, habitat change, has required that governments develop programs focused on

the removal of the predators or apparent competitors of caribou and justify such approaches as the most immediate and direct action to address small or rapidly declining populations of caribou (Ray et al., 2015; Serrouya et al., 2017). For wolves and cougars, and to lesser extent coyotes (*C. latrans*) and black bears (*Ursus americanus*), that has taken the form of lethal trapping, poisoning or aerial gunning (Bridger, 2019; Hayes et al., 2003; Hervieux et al., 2014; Lewis et al., 2017; Mosnier et al., 2008). Such activities are intensive and expensive and fraught with ecological, social, and ethical challenges (Brook et al., 2015; Immonen & Husby, 2016; Ray et al., 2015; Wallach et al., 2015).

Predator management is controversial and leads to conflict in perspectives and values for not only the public, but also conservation professionals that must evaluate and implement such actions (Brook et al., 2015; Musiani & Paquet, 2004). This raises questions about the extent to which such activities can serve as components of a viable strategy to recover endangered populations of caribou. In this article, we first review the scientific evidence that refutes or supports the application of predator management as a strategy for maintaining or increasing the abundance of small or declining populations of boreal and mountain caribou. We follow this by exploring the ethical challenges facing conservation scientists who wrestle with the philosophical conundrum of greatly reducing the abundance of one species to the benefit of a second, and the methods to achieve such outcomes. We bring these efficacy and ethical considerations together to evaluate the contribution of predator management to the conservation of woodland caribou in Canada.

We do not discuss predator management designed to benefit nonconservation values, such as increased game populations, reduced predation of livestock, or other human-centered objectives (Musiani & Paquet, 2004; Treves et al., 2019). Those efforts involve a different set of ecological and political considerations, ethical questions, and weighting of values, including the direct utility of wildlife (Boertje et al., 2010; Slagle et al., 2017). Also, given our positionality as non-Indigenous wildlife scientists, we do not provide any direct Indigenous perspectives related to predator management, including those activities designed to assist with the conservation of caribou (Lamb et al., 2022). Our interpretation of conservation-focused predator management is formed from nearly 50 years of collective experience studying the ecology and recovery of caribou in western, central, and eastern Canada. We hope that our perspective will contribute to a growing understanding of the ecological and ethical considerations of predator management when weighing recovery options for populations of this rapidly disappearing large mammal.

2 | ASSESSING THE EFFECTIVENESS OF PREDATOR MANAGEMENT

The effective implementation of predator management is dependent on a number of ecological conditions that dictate the predator–prey relationship. First, mortality must be the primary vital rate limiting population growth of the prey (Hegel et al., 2010). Thus, with sufficient reproduction, the abatement of predation-related mortality will result in an increase in the caribou population. In essence, nutrition or habitat is not limiting the growth of the population of interest (Russell, 2010). Second, predator management will be most effective in systems where the population dynamics of the primary predator has been decoupled from the abundance or availability of the prey. For example, if the decline of caribou regulates the predator population then there is little risk of a high density of predators and resulting predation leading to the extirpation of the caribou population (Klaczek et al., 2016). Although, any asynchrony in the population dynamics of the predator or prey, slow or limited reproductive output from the prey, or the availability of other prey species (i.e., apparent competition) could lead to extirpation. The broadly observed predator–prey dynamic between moose and deer, caribou, and their shared predators suggests that across much of their range caribou populations could be extirpated with relatively little change in the density of wolves, cougars, or other predators. The occurrence of apparent competition, by definition a decoupling of the dynamics of caribou from their primary predators, supports the second requirement for predator management (DeCesare et al., 2010; Hervieux et al., 2013; Serrouya et al., 2011; Wittmer et al., 2005).

When considering the first biological requirement, there is much theoretical and empirical evidence supporting the claim that unsustainable mortality is the most important vital rate limiting the population growth rate of woodland caribou. For instance, the fundamental population ecology of caribou suggests that adult female survival is the most important consideration when attempting to arrest population decline or increase the number of caribou (McLoughlin et al., 2003). The species is relatively long-lived and can reproduce at year 2 although the first calf at year 3 is more common (Adams et al., 2019; Bergerud, 1971). Reproductive senescence is limited until year 10 and caribou are known to reproduce in the wild until year 19 (Adams et al., 2019). Thus, a female caribou facing a low risk of mortality has the opportunity to produce many calves over a long life. The opposite would be true where adult female mortality is high. In some cases, a combination of low adult survival and high calf mortality can act in concert to limit population growth (Bergerud & Elliot, 1986; Lewis et al., 2017).

For many populations of caribou, the primary source of adult and calf mortality is predators. The supporting data are extensive and span 30 years of studies from across Canada. As examples, Seip (1992) reported that wolves and bears were the cause of 55% and 17% of known mortality of adult caribou in one population in southern British Columbia. Similarly, in southeastern British Columbia, bears followed by wolves were the primary predators and sources of mortality (Apps et al., 2013). In northeastern British Columbia, wolves were responsible or suspected to be responsible for 88% of the recorded mortality (Culling & Cichowski, 2017). In the southern Northwest Territories, 62% of total mortality of collared caribou were attributed to predators, mostly wolves (22% unidentified; Kelly, 2020). And in northeastern Alberta, wolves and other predators were responsible for 52% of total mortalities (29% unidentified; McLoughlin et al., 2003). Similar patterns of >60% mortality were attributed to wolves or other predators in southern Saskatchewan (Rettie & Messier, 1998), Ontario (Fryxell et al., 2020), and southern Quebec (Leclerc et al., 2014; Pinard et al., 2012). Where wolves are absent or extremely rare (e.g., Island of Newfoundland, Gaspé Peninsula of Quebec), coyotes and black bears are the primary source of mortality (>60%; Crête & Desrosiers, 1995; Lewis et al., 2017).

Some have suggested that habitat change and behavioral disturbance—a recognized threat to many populations of caribou (e.g., Johnson et al., 2015; Palm et al., 2020)—have resulted in bottom-up effects that have constrained population growth (Brown et al., 2007; Wasser et al., 2011). This argues that habitat change, either human caused or through natural disturbance, has resulted in a lack of forage that has caused population decline. However, most populations of woodland caribou now occur at historically low densities (Hervieux et al., 2013; Spalding, 2000). Moreover, there is little evidence of a density-dependent relationship between population abundance and reduced reproductive output or increased adult mortality, as might be expected following competition for nutritional resources (Eberhardt, 2002).

Although rates of parturition are not known for many populations of woodland caribou, most testing has revealed high pregnancy rates, often >90% (Adams et al., 2019; Culling & Cichowski, 2017; McLoughlin et al., 2003; Morineau et al., 2022; Rettie & Messier, 1998). Starvation or disease, possibly an outcome of nutritional deficiency, is not a commonly observed cause of mortality. Even the link between nutrition and predation has been difficult to prove. McLellan et al. (2012) found no relationship between predation, as a cause of mortality, and body condition. Finally, caribou produce only one calf during a birth year, not twins or triplets (Bergerud, 1971; Skoog, 1968). Conservation strategies focused on enhancing the abundance or quality of forage (e.g., rapid habitat restoration or supplementary feeding; Heard & Zimmerman, 2021), would not increase reproductive productivity in the form of multiple young as might be expected for other Cervidae (e.g., white-tailed deer, *O. virginianus*).

We are not suggesting that forage is unimportant for caribou. Woodland caribou, especially lactating females, have demonstrated nutritional limitations when using some plant communities, although the implications for population growth are not known (Denryter et al., 2018). Evidence from much larger populations of Arctic caribou (*R.t. groenlandicus*, *R.t. granti*) have revealed density-dependent nutritional effects, including annual or periodic pauses in reproduction (Cameron, 1994). However, for low-density populations of woodland caribou, the vast majority of direct and indirect evidence confirms that excessive mortality, in the form of predation, is the primary limiting factor (Hegel et al., 2010). Thus, theory suggests that a reduction in predation will result in an increase in survival and population growth. That expectation is supported by experimental work demonstrating that a reduction in predators can arrest the decline or increase the abundance of caribou.

Clark and Hebblewhite (2021) conducted a meta-analysis of predator removal designed to benefit the growth of ungulates in North America. Of the studies that they identified ($n = 62$), 12.9% were focused on woodland caribou. The response of caribou populations was greater than other species, and there was likely to be a positive effect for population growth. Considering the outcomes for individual populations, Bridger (2019) reported that following a significant reduction in the abundance of wolves, a number of populations of caribou in central British Columbia increased by 15% annually compared to an untreated, adjacent control population that continued to decline. Growth of the treatment populations corresponded with increased survival of adult female caribou and increased calf recruitment. In Alberta, wolf reduction arrested the decline of the Little Smoky population, but did not result in a positive growth rate (Hervieux et al., 2014). In southern Quebec, 8 years of wolf removal facilitated the reintroduction of caribou in the Charlevoix range, 50 years after its extirpation (St-Laurent & Dussault, 2012). It is important to note, however, that despite a decade of contemporary bear control, this population is again facing the risk of extirpation from human-mediated apparent competition, mostly driven by an intensification of timber harvesting.

Serrouya et al. (2019) reviewed the data for recovery actions of a number of populations of caribou in British Columbia and Alberta. They concluded that wolf

removal, in combination with other strategies designed to reduce predation (e.g., maternity penning), was effective for increasing the number of caribou. Harding et al. (2020) expressed concerns with those conclusions, arguing that there was no statistically robust or measurable relationship between wolf removal and population growth. They provided numerous criticisms of the analysis, including choice of study populations, inappropriate data for describing habitat loss, insufficient hypotheses for explaining population change, and incorrect protocols for assessing the strength of the statistical models. In spite of these misgivings, however, there is strong support for the qualitative conclusions of Serrouya et al. (2019) by independent analyses of the primary data for several of their study populations that have increased (Bridger, 2019; Lamb et al., 2022) or ceased their decline (Hervieux et al., 2014). Also, Harding et al. (2020) failed to provide supporting evidence for an alternative explanation of decline, other than to point to the necessity of considering "bottom-up" effects.

We agree that habitat change and loss is the ultimate cause of the decline of woodland caribou across the majority of their range. However, a considerable amount of evidence suggests that the mechanism of decline is increased mortality, not a reduction in reproduction as a product of nutritional limitations. There are likely complex habitat–predation interactions, where habitat change and human activities result in the displacement of caribou to areas with a greater risk of predation. Nonetheless, if human activities increase predation for caribou in any form, including displacement to riskier portions of the landscape, then one would expect efforts to reduce predation to have positive outcomes for the growth of caribou populations.

Serrouya et al. (2019) and Harding et al. (2020) are not the first to debate or test the efficacy of predator management as a strategy to increase numbers of caribou. There is now many decades of experience in applying and evaluating this approach (Clark & Hebblewhite, 2021). The Yukon and Alaska governments, for example, have implemented wolf reductions numerous times to support a range of management outcomes, including increased harvest of caribou and moose. These activities occurred across landscapes with relatively little habitat disturbance when compared to the southern distribution of woodland caribou. In one of the early studies from the Yukon, a reduction of wolves of 83%–86% resulted in a near doubling of the Finlayson population of caribou. That increase was influenced by reduced human harvest and favorable environmental conditions (Farnell, 2009). A 5-year wolf removal program for a further three populations resulted in a sustained increase in recruitment for one herd (Hayes et al., 2003). There was no statistical effect of wolf removal relative to increased adult survival, but two of the herds had pre-existing high survival (≥0.89) during the treatment period. In Alaska, formal wolf removal has occurred across portions of the state since 1975. In association with favorable weather, those efforts resulted in an increased rate of population growth for caribou and moose (Boertje et al., 1996). However, research in Alaska has shown that those efforts are effective only if wolves are the primary mechanism of mortality and when a large number of wolves are removed across an extensive area (Valkenburg et al., 2004).

Predator management has been effective in areas where species other than wolves are the top predators. In southeastern Québec, where wolves were extirpated >150 years ago (George, 1976), the predation exerted by coyotes and black bears was the main mortality agent for the Gaspésie population (Crête & Desrosiers, 1995), the last remnants of the Atlantic caribou. The first 15 years of predator management slowed population decline and greatly increased calf recruitment, although increasing timber harvest and resulting apparent competition has now negated decades of coyote and bear removal (Frenette et al., 2020). On the island of Newfoundland, wolves are extremely rare and coyotes have recently colonized much of caribou range. Predator management in the form of lethal removal of coyotes resulted in a significant increase in calf survival; diversionary feeding of black bears resulted in little to no effect (Lewis et al., 2017).

3 | LIMITATIONS AND COSTS OF PREDATOR MANAGEMENT

Numerous case studies suggest predator management is an effective strategy for arresting the immediate decline or even increasing populations of caribou (Bridger, 2019; Clark & Hebblewhite, 2021; Hervieux et al., 2014; Lewis et al., 2017). However, there are a range of ecological and logistical considerations that one must consider when evaluating the short-term, long-term, and practical efficacy of that approach. Most obvious among them, unsustainable predation must be a limiting factor and the primary cause of population decline. As a corollary to that fundamental premise, a predator management program must target the right predator. Many populations of caribou have multiple predators and in some systems wolf predation is not the most important limiting factor. For example, Johnson et al. (2019) demonstrated that further reduction of an already heavily trapped population of wolves would have no influence on the recovery of the Charlevoix population in southern Quebec. In that

system, as in others, black bears are an important, but opportunistic predator, mostly of calves. A small percentage of bears are thought to hunt caribou, but total calf mortality can be significant (Gustine et al., 2006; Leclerc et al., 2014; Pinard et al., 2012). Thus, management would need to focus on the few bears that were "specialist" predators of caribou, a daunting task when confronting large populations of bears (Bastille-Rousseau et al., 2011; Lesmerises et al., 2015). For caribou in British Columbia, wolves are likely the primary predator for northern populations, but cougar are more dominant at the southern distribution of the species (Apps et al., 2013). Thus, intensive wolf removal would have relatively little effect if there were no efforts to also reduce predation by cougar. At the same time, one needs to confirm that mortality from the primary predator is additive not compensatory to other factors that may regulate population growth (Bartmann et al., 1992). Additive mortality is likely the case for wolves preying on low-density populations of caribou that are well below their ecological carrying capacity, but that assumption should be tested.

As an additional consideration in evaluating the potential effectiveness of predator management, we must assume that caribou do not regulate the population dynamics of their predators. In some Arctic and northern boreal ecosystems, caribou is the major source of prey. Thus, declines in caribou result in concurrent declines in the abundance of their major predator, wolves (Klaczek et al., 2016; Neufeld et al., 2021). Given those ecological circumstances, predator management would be much less effective and lead to outcomes that are not comparable to the more southern distribution of woodland caribou where moose and deer are the primary source of prey biomass for predators (Latham et al., 2011; Serrouya et al., 2011). In those systems, habitat change and resulting apparent competition have decoupled the relationship between the abundance of caribou and their predators.

To be effective, predator management must be intensive and extensive across both geography and time. Failed efforts often are attributed to the removal of too few predators over too small of an area or a lack of sustained effort (Valkenburg et al., 2004). Wolves can compensate for a high rate of mortality, showing little population change even following a 29%–40% annual reduction through human harvest (Adams et al., 2008; Hayes et al., 2003; Peterson et al., 1984; Webb et al., 2011). For example, Hervieux et al. (2014) reported no change in annual removal rates of wolves even following intensive removal (>100 wolves/year) over a 7-year period. The mechanism for that demographic response is often immigration (i.e., spillover predation) or increased reproduction resulting from a lack of intraspecific competition for prey (Adams et al., 2008; Frenette et al., 2020). Similarly, where prey is abundant, coyotes can support annual mortality rates as high as ~40% without noticeable changes in population density (Knowlton, 1972).

Following a review of wolf management programs in western North America, Russell (2010) concluded that wolf removal would only be effective if 65%–80% of wolves were removed over a sufficient area and time, typically >4 years. For caribou populations in western Canada, that has meant the lethal removal of >100 wolves per year (Bridger, 2019; Hervieux et al., 2014), and even that might be insufficient for high density or fecund populations of wolves that are supported by abundant prey. Both the intensity, spatial extent, and duration of a predator management program depends on many factors associated with the population of interest, including the extent of habitat loss and conversion, and the corresponding type, distribution, and density of the predator.

Past experience tells us that short-term predator management is not an effective strategy for the long-term conservation and recovery of caribou. The growth of a wolf population is dependent on the biomass of ungulate prey (Kuzyk & Hatter, 2014). The increase in caribou, and more importantly moose and deer, will support rapid growth of wolf populations following the end of a reduction program. That is contingent on the wolf population not being regulated by some other factor. In the case of the Finlayson population of the Yukon, wolves increased between control years and returned to prereduction densities rapidly following the end of the program (Farnell, 2009). The annual return of wolves and coyotes to the ranges of the Little Smoky and Gaspésie populations, respectively, is further evidence of the resilience of canids to control efforts, and their ability to quickly reoccupy ranges from which they were removed. The other predators of caribou—including black bear, grizzly bear (*U. arctos*), Canada lynx (*Lynx canadensis*), and wolverine (*Gulo gulo*)—are less fecund, but again control activities likely offer short-term reprieve from unsustainable predation.

Given the fundamental ecology of caribou, we should expect small populations to resume their former trajectory of decline following the cessation of a predator reduction program. This means that in addition to stopgap predator management, the underlying mechanism for excessive predation must be addressed. For many populations of caribou, that will require habitat restoration or recovery that reduces the carrying capacity of ungulates or the hunting efficiency of the predator. Although, given the cost and the many thousands of kilometers of roads and seismic lines as well as the extensive

areas of burned and cut forest found within caribou range, anything beyond strategic restoration is impractical or at the very least will take decades to achieve (Dickie et al., 2021; Johnson et al., 2019; Lacerte et al., 2021; Nagy-Reis et al., 2021).

A comprehensive predator management program has many obvious and unpredicted costs, both ecological and economic. As reported for the Yellowstone (Beschta & Ripple, 2016) and other ecosystems (Hebblewhite et al., 2005), the removal of an apex predator can result in novel and unpredicted ecological outcomes. Reducing the abundance of high trophic-level species like wolves could modify the structure or composition of communities, even leading to the collateral extirpation of other species (Hebblewhite et al., 2005; Prugh et al., 2009). Similarly, the release of large herbivores can restructure the plant community and allow niche-space for other carnivores (Prugh et al., 2009). What is not clear, however, is the time required for predator suppression to fundamentally restructure plant and animal communities. In comparison to the Yellowstone Ecosystem, where wolves were completely absent for approximately 70 years, a 5- to 10-year wolf removal program might have relatively little long-term effect. Moreover, recent predator reduction programs for wolves have not achieved the complete long-term extirpation of the species, as was observed across much of the United States during the 19th and 20th centuries.

Intensive predator management over a large area with few roads is neither simple nor inexpensive. A focused and consistent effort is required to decrease the abundance of wolves by >65%, the typical target for reduction. Trapping is only practical in areas with ground access and often there is insufficient harvest to reduce populations of wolves (Webb et al., 2011). Aerial gunning can require considerable helicopter time, a significant expense, when the area is heavily forested. Toxicant bait stations have been used by many jurisdictions, but they require consistent monitoring, helicopter access, and result in the death of nontarget species (Hervieux et al., 2014).

The economic cost of predator management is not insignificant, but will vary according to the level of intensity and the size and accessibility of the control area. For the Little Smoky population, the cost was estimated at \$35/km^2 (Canadian dollars; Schneider et al., (2010). Johnson et al. (2019) applied that cost to a simulated 50-year wolf removal program for the Chinchaga population of British Columbia. They estimated a total cost of \$16.9 million dollars or \$25,665 per net caribou gained by the population. That was the most cost-effective recovery method they modeled. Nagy-Reis et al. (2020) developed a different population model, but came to the same result: wolf removal resulted in the greatest population growth at the lowest cost. The annual cost for 3 years of a wolf removal program for three populations of caribou in British Columbia ranged from \$475,000 to \$340,000. That followed two considerably more expensive years (e.g., \$800,000) when methods were being refined (Bridger, 2019). For the Gaspésie population of southeastern Quebec, the trapping of ~78 coyotes and ~49 bears each year (from May to October) from the immediate area surrounding the Gaspésie National Park (802 km^2) cost ~\$87,000 annually. Considering that this predator management program has been in continuous operation since 2001, that represents a considerable amount of time and money. Yet, the outcome is a slowing of the pace of extinction, rather than a stable or recovering population (Frenette et al., 2020).

4 | ETHICAL, PHILOSOPHICAL, AND SOCIAL DIMENSIONS OF PREDATOR MANAGEMENT

Carnivores, particularly large-bodied predators, have been a source of fear and conflict for humans since time immemorial, and as a result have been subjected to persecution, retaliation, and targeted pursuit (Musiani & Paquet, 2004). Direct mortality, prey depletion, and habitat loss have led to range contractions and population declines of many species around the world (Wolf & Ripple, 2017). Although wolves, bears, and cougars have exhibited profound range loss since the settlement of Europeans in North America, in recent decades, populations have responded positively to recovery efforts (Gompper et al., 2015). The conservation of carnivores is supported by a growing appreciation for their functional role within ecosystems and their enhanced public appeal as charismatic symbols of wilderness and nature (Bergstrom, 2017; Ray et al., 2005). Despite such broad-scale success, real and perceived conflicts prevail in rural or agricultural areas (Houston et al., 2010). Often that conflict increases in tandem with even modest increases in predator numbers (Lamb et al., 2020; Treves et al., 2019).

Against this backdrop, predator management has a long history that is steeped in human attitudes toward predators, defense of property, and perceptions of competition with game and livestock (Bergstrom, 2017; Treves et al., 2019). For wolves in particular, the context is and always has been somewhat different for those living outside and inside agricultural areas. Where livestock production is not a priority, wolf management is generally governed by concerns for wild ungulate populations that are managed to meet the consumptive needs of humans

(Boertje et al., 2010). Across much of northern Canada and Alaska, wolves are not considered to be a species of conservation concern. As such, their hunting and trapping is not subject to many restrictions (Musiani & Paquet, 2004). This set of circumstance facilitates the idea of wolf removal as a common and acceptable action to manage Threatened and Endangered caribou populations. Alternatively, given overall positive public attitudes toward predator conservation and their precarious status and history of persecution elsewhere, it should not be surprising that such government-sponsored programs have been the source of considerable negative attention, even inviting the engagement of celebrities (News, 2015).

Within the scientific community, there is much conflict and many discussions about the ethics of predator management. In fact, arguments that focus on scientific issues are difficult to isolate from expressions of the values of the public and the ethical and philosophical questions that face conservation professionals (Boertje et al., 2010). Yet, in this circumstance, it is essential to distinguish, understand, and debate the ethics of predator management relative to questions about the effectiveness and reasons for such actions. McLaren (2016), for example, reviewed a number of lethal and nonlethal methods for direct reduction of wolves within four jurisdictions in Canada. They reported myriad issues focused on the ethics of such activities, but offered no conclusions other than that these are "equally as important" to consider as the viability, effectiveness, cost, and political and public support of wolf removal.

Brook et al. (2015) provided a critical review of predator management in support of caribou conservation with a particular emphasis on aerial gunning and poisoning. To mention just a few, the authors pointed out the virtual impossibility of rapidly and humanely killing individual wolves from the air. The ingestion of bait laced with strychnine not only results in wounding of target animals, but the killing of many individuals of nontarget species (see also Bergstrom, 2017; Hervieux et al., 2014). These methods are not among those considered to be "humane" for euthanizing wolves or any animals used in research (sensu Canadian Council on Animal Care, 2010), raising questions as to whether scientists can even study and monitor predator management if it does not meet ethical standards for working with wildlife (Brook et al., 2015). Even if members of the public support predator management, Slagle et al. (2017) documented increased discomfort with the humaneness of wildlife management techniques used to manage predators. Add to this, the growing demands that killing a sentient creature deserves at least some direct moral consideration (Coghlan & Cardilini, 2021; Fox & Bekoff, 2011).

Our review of this topic brings up important questions with respect to the inhumane treatment of one species for the advantage of another. We are not evaluating predator management in the most common context within which it is deployed (e.g., agricultural conflict), rather focusing attention on this as an action used to save almost-extirpated caribou populations. However, we must ask: does that matter? Proponents of "compassionate conservation" would argue that no matter what the circumstances, four guiding principles—first do no harm, individuals matter, peaceful coexistence, and inclusivity—should govern conservation practices (Coghlan & Cardilini, 2021). Even so, we must recognize that irresolvable conservation dilemmas can lead to conflicting moral claims that may require a "nuanced ethic" (Batavia et al., 2020).

When it comes to the deteriorating status of woodland caribou, there is indeed a different set of ethical considerations from those associated with wolves. For one thing, caribou are Endangered or Threatened and disappearing across much of their range. In comparison, wolves are not a species of conservation concern across most caribou ranges and they are resilient to high levels of harvest (Adams et al., 2008; National Research Council, 1997). That removes much of the concern of focused predator management resulting in the extirpation or loss of wolves, as was the history for the species across much of the United States (Musiani & Paquet, 2004). Nonetheless, the simple argument that we must reduce wolves to save endangered caribou can ring shallow.

The current emphasis on predator management by some jurisdictions is emblematic of many missed opportunities to address the gradual disappearance of a species at risk. By the time managers turn to predator reduction as a means to reverse the decline of caribou populations, multiple warning signals have already flashed. Even with mounting empirical evidence that confirms a relationship between habitat loss and population decline, industrial disturbance has accelerated over the past several decades since caribou declines were first documented (Environment Canada, 2012; Johnson et al., 2015, 2020; Nagy-Reis et al., 2021; Rempel et al., 2021; Rudolph et al., 2017). Governments have relied on piecemeal mitigation of impacts, rather than limitation of the industrial footprint, long after caribou were legally recognized as Threatened or Endangered. Recovery of populations in this context of continued industrial-scale habitat removal has continued with weak regulations that have by and large failed to compel meaningful levels of habitat protection and restoration (Collard et al., 2020; Nagy-Reis et al., 2021). Even where parcels of land have been set aside for caribou, those habitat or conservation areas are of insufficient size or they are placed in areas that fail to

mitigate shifting predator–prey dynamics (Nagy-Reis et al., 2021). Wolf removal is viewed by many as more economical than restoring or protecting habitats (Johnson et al., 2019; Nagy-Reis et al., 2020), given the opportunity costs (e.g., revenue from natural resource extraction) associated with the latter (Schneider et al., 2010). Thus, this conservation crisis offers its own unique ethical dilemma when one considers the continuing sacrifice of wolves, bears, and coyotes as a "solution" that facilitates further habitat loss for caribou.

Predator management was deployed in western Canada starting in the 1940s and much earlier in the eastern portion of the country (Bergerud & Elliot, 1986). However, it was not until the early 2000s that concerns about the extirpation of rapidly declining populations of caribou spurred governments to initiate intensive and systematic predator management in the name of conservation (Hervieux et al., 2014). We are now at a point where intensive or manipulative conservation actions are the only options to stave off extirpation of small and rapidly declining populations (Hervieux et al., 2014). Even within protected areas, which in parts of caribou range are isolated and surrounded by roads and other human activities, conservation professionals must resort to predator control and other forms of potentially controversial management (Frenette et al., 2020; Parks Canada Agency, 2017; St-Laurent & Dussault, 2012).

5 | COMPLEX REALITY OF PREDATOR MANAGEMENT AS A CONSERVATION ACTION

There are multiple reasons for delaying or simply not acting to save endangered species (McDevitt-Irwin et al., 2015; Ferreira et al., 2019), but in the case of caribou that long list does not include ignorance. Considerable research and monitoring have clearly documented both the short- and long-term declines of the subspecies (Courtois et al., 2003; Hervieux et al., 2013; Johnson et al., 2015; Santomauro et al., 2012; Schaefer, 2003; Seip, 1992). Those trends in decline, and the associated risks to persistence, have been confirmed by multiple provincial and federal assessment processes that now span nearly 20 years of recovery planning. As examples, populations belonging to "designatable units" (sensu COSEWIC, 2014b, 2014a) of woodland caribou in western Canada were formally recognized as species at risk when the federal Species at Risk Act came into force in 2003. Despite those protections on paper, we continue to observe population extirpation. The recent loss of at least six populations of mountain caribou from British Columbia and Alberta and the last of the caribou in the contiguous United States have revealed the absence of meaningful action thus far.

Governments in Canada have failed to make difficult decisions in the past for the conservation of caribou today. The calculus of delay that many have applied to caribou conservation was largely based on the socioeconomic costs of the now rather than a consideration of the long-term decline of the species and the resulting desperate, controversial, and costly recovery actions in the future. However, theory and general lessons from population and conservation ecology tells us that it takes longer and costs more to grow a small remnant population of caribou to a level of abundance that is thought to be sustainable. Also, small populations are inherently more at risk of being lost (O'Grady et al., 2004). The extirpation of the last caribou in Banff National Park demonstrated the harsh reality of environmental stochasticity (DeCesare et al., 2011). Finally, populations with few individuals limit the practicality of some recovery actions, including captive breeding and translocation, which are dependent on source or donor populations.

There is broad appreciation that at risk species become more endangered with delay and the eventual responses have less certainty of success and greater costs to governments and society (Ferreira et al., 2019; Frank & Wilcove, 2019). Seldom discussed is the relationship between delay and the increase in the magnitude or number of ethical considerations that accompany evermore desperate recovery actions. That is demonstrated by the worsening caribou crisis in Canada. The increasing decline and disappearance of populations have resulted in more intensive conservation responses that are accompanied by arguments that extend beyond just ecological efficacy (Brook et al., 2015). Yet, predator control is not the only ethically debatable and potentially objectionable action currently in practice or under consideration within the realm of caribou conservation.

The concept of conservation triage is being more widely debated as the number of small and unsustainable populations of caribou increases (Schneider et al., 2010). Triage would require governments to prioritize some populations for recovery while allowing others to become extirpated. However, absent strong agreement and clear rules on how to define the giving-up point, there can be no assurance of avoiding ever-increasing slippage of what governments and society are willing to relegate to the collection of populations that are deemed unrecoverable. The acceptance of triage could even provide perverse incentives for this outcome, as exemplified by the disturbingly common frequency with which decisions to approve major industrial projects have used the rationale that caribou habitat in the project area was already degraded or caribou were extirpated (Collard et al., 2020).

Even if the choice is made to recover all populations, there are considerable ethical questions about untested and more desperate actions. As examples, there has been some experimentation and now much consideration of managing the third species in the apparent competition triangle: moose (Serrouya et al., 2017). However, the reduction of moose through direct harvest or management of habitat risks further limitations on the cultural and subsistence activities of Indigenous communities that at one time relied on caribou. Captive breeding and translocation are expensive and there are few examples of long-term population recovery (Grant et al., 2019; Leech et al., 2017; St-Laurent & Dussault, 2012). Also, in many locations, there are now too few caribou to support in situ and ex situ populations. Some captive breeding proposals require the removal of the last free-ranging caribou, effectively extirpating small populations with an uncertain hope of future replacement. As demonstrated by the California condor (*Gymnogyps californianus*), removing the last of a species from the wild can lead to considerable controversy and debate (Cohn, 1993). More novel is the long-term shepherding of large groups of caribou in fenced, predator-free areas of 30–100 km^2 (Government of Alberta, 2017). This intensive and expensive action will set a new benchmark for what is acceptable ex situ conservation and may result in unwanted or unintended ecological and evolutionary legacies, including giving license for further loss of habitat and the general degradation of the caribou ecosystem.

The efficacy and ethics of predator management have been discussed by conservation and management professionals for decades, yet we are no closer in finding consensus on the acceptability of such practices (Anderson, 2021; Clark & Hebblewhite, 2021; National Research Council, 1997; Slagle et al., 2017). Justifications such as "wolves are nowhere near endangered or threatened in Canada" or "there is a long history of predator (and prey) reduction to recover endangered species" (Serrouya et al., 2019; 6184) are not compelling arguments for those who find many of the methods of control as inhumane or that have deep philosophical objections to killing one species to save another (Brook et al., 2015; Fox & Bekoff, 2011). Although there is considerable evidence to support the tactical use of predator management as one tool for maintaining caribou over the short-term (Bridger, 2019; Hervieux et al., 2014; McNay et al., 2022; Russell, 2010), there is no graceful way to divorce efficacy from the values held by society and the normative or prescriptive ethics that guide our activities as conservation professionals.

Although the debate is often focused on those that critique or object to predator management, there are some natural resource and conservation professionals, members of the public, and Indigenous Nations who support the removal of wolves or other predators as a necessary means to an end (Lamb et al., 2022; Serrouya et al., 2019). As we have argued, removal of wolves can result in an increase in caribou populations over the short term. Also, when compared to other options, including habitat restoration, predator management is one of the most direct and inexpensive methods (Johnson et al., 2019). That is particularly the case when considering the economic implications of restricting forestry or oil and gas operations across large areas that serve as habitat for caribou (Hebblewhite, 2017).

Efficacy and ethics are foundational elements that justify and support our work, including the conservation of caribou, within the public realm. Thus, it is important to not conflate those intrinsically related, yet independent considerations. An activity can be considered effective, but also unethical. An activity deemed unethical by some does not by definition dismiss the value of that action for the conservation of a species that is facing extinction. The challenge is deciding collectively on the acceptability of such practices to recover endangered species or when deemed acceptable the type and method of predator management. These ethical questions are much more difficult to resolve than arguments about the ecological efficacy of wolf removal that focus on the consideration of experimental design, statistical significance or monitoring protocol (e.g., Clark & Hebblewhite, 2021; Harding et al., 2020; Serrouya et al., 2019).

There are a range of recovery actions for imperiled populations of caribou, some tried and tested, and some waiting for experimentation (Ray et al., 2015). Multiple actions will need to work in concert once a population becomes small and imperiled, and some may no longer be practical (Serrouya et al., 2019). Those immediate solutions, however, can only be effective if they offer a bridge to habitat recovery that no longer supports human-mediated apparent competition, which will take decades. At present, predator management, like maternity pens and captive breeding, are being deployed by governments as a means to mitigate continued habitat clearing within caribou ranges, with little accompanying investment in restoration—effectively, a bridge to nowhere.

Ultimately, conservation professionals and broader society must ask if "the means justify the ends" when considering the application of predator management or other invasive practices to ensuring the persistence of woodland caribou. Surely legal status as a Threatened or Endangered species is a meaningful representation of society's will to conserve biodiversity generally and caribou in particular. The direct financial costs of recovery, including predator management, but also restoration activities, are significant,

but trivial in the context of the billions of dollars of revenue and taxation generated by industry that "shares" caribou range (Hebblewhite, 2017). In a rich country such as Canada, that has taken so much wealth from natural systems, there should be financial resources to implement these recovery actions. Inevitably, however, delay in working to better manage the large landscapes needed by caribou will lead to a greater emphasis on short-term, stop-gap measures and a deepening of the ethical dilemmas that we have outlined here. That is the history of this conservation crisis and likely the future story for caribou. If we had acted when caribou were first assessed as a species at risk of extinction, we might not be discussing the ethical perils of predator management—an activity that buys time, but is not a solution.

AUTHOR CONTRIBUTIONS

Chris J. Johnson, Justina C. Ray, and Martin-Hugues St-Laurent initiated and developed the ideas for the paper. Chris J. Johnson led the writing with major contributions of text and conceptualization of the document from Justina C. Ray, and Martin-Hugues St-Laurent.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

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No data were used to formulate this manuscript.

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The authors are not aware of any ethical issues regarding this work.

ORCID


Chris J. Johnson https://orcid.org/0000-0002-4044-6993

REFERENCES

Adams, L. G., Farnell, R., Oakley, M. P., Jung, T. S., Larocque, L. L., Lortie, G. M., Mclelland, J., Reid, M. E., Roffler, G. H., & Russell, D. E. (2019). Evaluation of maternal penning to improve calf survival in the Chisana caribou herd. *Wildlife Monographs*, *204*, 5–46.

Adams, L. G., Stephenson, R. O., Dale, B. W., Ahgook, R. T., & Demma, D. J. (2008). Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. *Wildlife Monographs*, *170*, 1–25.

Anderson, R. M. (2021). Killing for the common good? The (bio)politics of wolf management in Washington state. *Elementa: Science of the Anthropocene*, *9*, 00179. https://doi.org/10.1525/elementa.2020.00179

Apps, C. D., Mclellan, B. N., Kinley, T. A., Serrouya, R., Seip, D. R., & Wittmer, H. U. (2013). Spatial factors related to mortality and population decline of endangered mountain caribou. *The Journal of Wildlife Management*, *77*, 1409–1419.

Barber, Q. E., Parisien, M. A., Whitman, E., Stralberg, D., Johnson, C. J., St-Laurent, M. H., DeLancey, E. R., Price, D. T., Arseneault, D., Wang, X., & Flannigan, M. D. (2018). Potential impacts of climate change on the habitat of boreal woodland caribou. *Ecosphere*, *9*, e02472.

Bartmann, R. M., White, G. C., & Carpenter, L. H. (1992). Compensatory mortality in a Colorado mule deer population. *Wildlife Monographs*, *121*, 1–39.

Bastille-Rousseau, G., Fortin, D., Dussault, C., Courtois, R., & Ouellet, J.-P. (2011). Foraging strategies by omnivores: Are black bears actively searching for ungulate neonates or are they simply opportunistic predators? *Ecography*, *34*, 588–596.

Batavia, C., Nelson, M. P., & Wallach, A. D. (2020). The moral residue of conservation. *Conservation Biology*, *34*, 1114–1121.

Bergerud, A. T. (1971). The population dynamics of Newfoundland caribou. *Wildlife Monographs*, *25*, 3–55.

Bergerud, A. T., & Elliot, J. P. (1986). Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology*, *64*, 1515–1529.

Bergerud, A. T., Luttich, S. N., & Camps, L. (2008). *The return of Caribou to Ungava*. McGill-Queen's University Press.

Bergstrom, B. J. (2017). Carnivore conservation: Shifting the paradigm from control to coexistence. *Journal of Mammalogy*, *98*, 1–6.

Beschta, R. L., & Ripple, W. J. (2016). Riparian vegetation recovery in Yellowstone: The first two decades after wolf reintroduction. *Biological Conservation*, *198*, 93–103.

Blagdon, D., & Johnson, C. J. (2021). Short term, but high risk of predation for endangered mountain caribou during seasonal migration. *Biodiversity and Conservation*, *30*, 719–739.

Boertje, R. D., Keech, M. A., & Paragi, T. F. (2010). Science and values influencing predator control for Alaska moose management. *The Journal of Wildlife Management*, *74*, 917–928.

Boertje, R. D., Valkenburg, P., & McNay, M. E. (1996). Increases in moose, caribou, and wolves following wolf control in Alaska. *The Journal of Wildlife Management*, *60*, 474–489.

Bridger. (2019). *South peace caribou recovery following five years of experimental wolf reduction*. Canada.

Brook, R., Cattet, M., Darimont, C., Paquet, P., & Proulx, G. (2015). Maintaining ethical standards during conservation crises. *Canadian Wildlife Biology and Management*, *4*, 72–79.

Brook, B.W., Sodhi, N.S., & Bradshaw, C.J.A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology and Evolution*, *23*, 453–460.

Brown, G. S., Landriault, L., Sleep, D. J. H., & Mallory, F. F. (2007). Comment arising from a paper by Wittmer et al.: Hypothesis testing for top-down and bottom-up effects in woodland caribou population dynamics. *Oecologia*, *154*, 485–492.

Cameron, R. D. (1994). Reproductive pauses by female caribou. *Journal of Mammalogy*, *75*, 10–13.

Canadian Council on Animal Care. (2010). *CCAC guidelines on: Euthanasia of animals used in science*. Canadian Council on Animal Care.

Clark, T. J., & Hebblewhite, M. (2021). Predator control may not increase ungulate populations in the future: A formal meta-analysis. *Journal of Applied Ecology*, *58*, 812–824.

Coghlan, S., & Cardilini, A. P. A. (2021). A critical review of the compassionate conservation debate. *Conservation Biology*, *36*, e13760. https://doi.org/10.1111/cobi.13760

Cohn, J. P. (1993). The flight of the California condor. *Bioscience*, *43*, 206–209.

Collard, R.-C., Dempsey, J., & Holmberg, M. (2020). Extirpation despite regulation? Environmental assessment and caribou. *Conservation Science and Practice*, *2*, e166.

COSEWIC. (2014a). *COSEWIC assessment and status report on the Caribou Rangifer tarandus, Northern Mountain population, Central Mountain population and Southern Mountain population in Canada* (p. 113). Committee on the Status of Endangered Wildlife in Canada.

COSEWIC. (2014b). *COSEWIC assessment and status report on the Caribou Rangifer tarandus, Newfoundland population, Atlantic-Gaspésie population and Boreal population, in Canada* (p. 128). Committee on the Status of Endangered Wildlife in Canada.

Courtois, R., Ouellet, J.-P., Gingras, A., Dussault, A., Breton, L., & Maltais, J. (2003). Historical changes and current distribution of Caribou, Rangifer tarandus, in Quebec. *Canadian Field-Naturalist*, *117*, 399–414.

Crête, M., & Desrosiers, A. (1995). Range expansion of coyotes, Canis latrans, threatens a remnant herd of caribou, Rangifer tarandus, in southeastern Quebec. *Canadian Field-Naturalist*, *10*, 227–235.

Crowley, S. L., Hinchliffe, S., & McDonald, R. A. (2017). Invasive species management will benefit from social impact assessment. *Journal of Applied Ecology*, *54*, 351–357.

Culling, D., & Cichowski, D. B. (2017). *Boreal Caribou (Rangifer tarandus) in British Columbia: 2017 science review*. British Columbia Oil and Gas Research and Innovation Society.

Cupp, A. R., Woiak, Z., Erickson, R. A., Amberg, J. J., & Gaikowski, M. P. (2017). Carbon dioxide as an under-ice lethal control for invasive fishes. *Biological Invasions*, *19*, 2543–2552.

Dawe, K. L., & Boutin, S. (2016). Climate change is the primary driver of white-tailed deer (*Odocoileus virginianus*) range expansion at the northern extent of its range; land use is secondary. *Ecology and Evolution*, *6*, 6435–6451.

DeCesare, N. J., Hebblewhite, M., Robinson, H. S., & Musiani, M. (2010). Endangered, apparently: The role of apparent competition in endangered species conservation. *Animal Conservation*, *13*, 353–362.

DeCesare, N. J., Whittington, J., Hebblewhite, M., Robinson, H. S., Bradley, M., Neufeld, L., & Musiani, M. (2011). The role of translocation in recovery of woodland caribou populations. *Conservation Biology*, *25*, 365–373.

Denryter, K. A., Cook, R. C., Cook, J. G., Parker, K. L., & Gillingham, M. P. (2018). *Nutritional values of habitats for woodland caribou during summer (Research Extension Note)*. Natural Resources and Environmental Studies Institute, University of Northern British Columbia.

Dickie, M., McNay, R. S., Sutherland, G. D., Sherman, G. G., & Cody, M. (2021). Multiple lines of evidence for predator and prey responses to caribou habitat restoration. *Biological Conservation*, *256*, 109032.

Diller, L. V., Hamm, K. A., Early, D. A., Lamphear, D. W., Dugger, K. M., Yackulic, C. B., Schwarz, C. J., Carlson, P. C., & McDonald, T. L. (2016). Demographic response of northern spotted owls to barred owl removal. *The Journal of Wildlife Management*, *80*, 691–707.

Eberhardt, L. L. (2002). A paradigm for population analysis of long-lived vertebrates. *Ecology*, *83*, 2841–2854.

Environment Canada. (2012). *Recovery strategy for the woodland Caribou (Rangifer tarandus caribou), boreal population, in Canada*. Species at risk act recovery strategy series. Environment Canada.

Farnell R. (2009). Three decades of Caribou Recovery Programs in Yukon: A paradigm shift in wildlife management. Yukon Fish and Wildlife Report MRC-09-01. Yukon Government, Whitehorse, Yukon, Canada.

Ferreira, C. C., Hossie, T. J., Jenkins, D. A., Wehtje, M., Austin, C. E., Boudreau, M. R., Chan, K., Clement, A., Hrynyk, M., Longhi, J., MacFarlane, S., Majchrzak, Y. N., Otis, J. A., Peers, M. J. L., Rae, J., Seguin, J. L., Walker, S., Watt, C., & Murray, D. L. (2019). The recovery illusion: What is delaying the rescue of imperiled species? *Bioscience*, *69*, 1028–1034.

Fox, C. H., & Bekoff, M. (2011). Integrating values and ethics into wildlife policy and management-lessons from North America. *Animals*, *1*, 126–143.

Frank, E. G., & Wilcove, D. S. (2019). Long delays in banning trade in threatened species. *Science*, *363*, 686–688.

Frenette, J., Pelletier, F., & St-Laurent, M.-H. (2020). Linking habitat, predators and alternative prey to explain recruitment variations of an endangered caribou population. *Global Ecology and Conservation*, *22*, e00920.

Fryxell, J. M., Avgar, T., Liu, B., Baker, J. A., Rodgers, A. R., Shuter, J., Thompson, I. D., Reid, D. E. B., Kittle, A. M., Mosser, A., Newmaster, S. G., Nudds, T. D., Street, G. M., Brown, G. S., & Patterson, B. (2020). Anthropogenic disturbance and population viability of woodland caribou in Ontario. *The Journal of Wildlife Management*, *84*, 636–650.

George, S. (1976). A range extension of coyote in Québec. *Canadian Field-Naturalist*, *90*, 78–79.

Gompper, M. E., Belant, J. L., & Kays, R. (2015). Carnivore coexistence: America's recovery. *Science*, *347*, 382–383.

Government of Alberta. (2017). *Draft provincial woodland Caribou range plan*. Government of Alberta.

Government of BC. (2018). Provincial Caribou Recovery Program – Discussion Paper. Ministry of Forests, Lands and Natural Resources Operations and Rural Development, Victoria, British Columbia, Canada.

Govindarajulu, P., Altwegg, R., & Anholt, B. R. (2005). Matrix model investigation of invasive species control: Bullfrogs on Vancouver Island. *Ecological Applications*, *15*, 2161–2170.

Grant, L., Johnson, C., & Thiessen, C. (2019). Evaluating the efficacy of translocation: Maintaining habitat key to long-term success for an imperiled population of an at-risk species. *Biodiversity and Conservation*, *28*, 2727–2743.

Gustine, D. L., Parker, K. L., Lay, R., Gillingham, M. P., & Heard, D. C. (2006). Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs*, *165*, 1–32.

Hampton, J. O., Warburton, B., & Sandøe, P. (2019). Compassionate versus consequentialist conservation. *Conservation Biology*, *33*, 751–759.

Harding, L. E., Bourbonnais, M., Cook, A. T., Spribille, T., Wagner, V., & Darimont, C. (2020). No statistical support for wolf control and maternal penning as conservation measures for endangered mountain caribou. *Biodiversity and Conservation*, *29*, 3051–3060.

Hayes, R. D., Farnell, R., Ward, R. M. P., Carey, J., Dehn, M., Kuzyk, G. W., Baer, A. M., Gardner, C. L., & O'Donoghue, M. (2003). Experimental reduction of wolves in the Yukon: Ungulate responses and management implications. *Wildlife Monographs*, *152*, 1–35.

Heard, D. C., & Zimmerman, K. L. (2021). Fall supplemental feeding increases population growth rate of an endangered caribou herd. *PeerJ*, *9*, e10708.

Hebblewhite, M. (2017). Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. *Biological Conservation*, *206*, 102–111.

Hebblewhite, M., White, C. A., Nietvelt, C. G., McKenzie, J. A., Hurd, T. E., Fryxell, J. M., Bayley, S. E., & Paquet, P. C. (2005). Human activity mediates a trophic cascade caused by wolves. *Ecology*, *86*, 2135–2144.

Hegel, T. M., Mysterud, A., Huettmann, F., & Stenseth, N. C. (2010). Interacting effect of wolves and climate on recruitment in a northern mountain caribou population. *Oikos*, *119*, 1453–1461.

Hervieux, D., Hebblewhite, M., DeCesare, N. J., Russell, M., Smith, K., Robertson, S., & Boutin, S. (2013). Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. *Canadian Journal of Zoology*, *91*, 872–882.

Hervieux, D., Hebblewhite, M., Stepnisky, D., Bacon, M., & Boutin, S. (2014). Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus caribou*) in Alberta. *Canadian Journal of Zoology*, *92*, 1029–1037.

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, *12*, 197–229.

Holt, R. D. (1984). Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *The American Naturalist*, *124*, 377–406.

Houston, M. J., Bruskotter, J. T., & Fan, D. (2010). Attitudes toward wolves in the United States and Canada: A content analysis of the print news media, 1999–2008. *Human Dimensions of Wildlife*, *15*, 389–403.

Immonen, E., & Husby, A. (2016). Norway wolf cull will hit genetic diversity. *Nature*, *539*, 31.

Johnson, C. A., Sutherland, G. D., Neave, E., Leblond, M., Kirby, P., Superbie, C., & McLoughlin, P. D. (2020). Science to inform policy: Linking population dynamics to habitat for a threatened species in Canada. *Journal of Applied Ecology*, *57*, 1314–1327.

Johnson, C. J., Ehlers, L. P. W., & Seip, D. R. (2015). Witnessing extinction – Cumulative impacts across landscapes and the future loss of an evolutionarily significant unit of woodland caribou in Canada. *Biological Conservation*, *186*, 176–186.

Johnson, C. J., Mumma, M. A., & St-Laurent, M. (2019). Modeling multispecies predator–prey dynamics: Predicting the outcomes of conservation actions for woodland caribou. *Ecosphere*, *10*, e02622.

Kelly A. (2020). Seasonal patterns of mortality for boreal caribou (Rangifer tarandus caribou) in an intact environment. MSc Thesis. University of Alberta, Edmonton, Alberta, Canada. https://era.library.ualberta.ca/items/fcffc2d5-cfb2-4128-bf5e-9cddf0091949

Klaczek, M. R., Johnson, C. J., & Cluff, H. D. (2016). Wolf-caribou dynamics within the central Canadian Arctic: Wolf-Caribou dynamics. *The Journal of Wildlife Management*, *80*, 837–849.

Knowlton, F. F. (1972). Preliminary interpretations of coyote population mechanics with some management implications. *The Journal of Wildlife Management*, *36*, 369–382.

Kuzyk, G. W., & Hatter, I. W. (2014). Using ungulate biomass to estimate abundance of wolves in British Columbia. *Wildlife Society Bulletin*, *38*, 878–883.

Lacerte, R., Leblond, M., & St-Laurent, M.-H. (2021). Determinants of vegetation regeneration on forest roads following restoration treatments: Implications for boreal caribou conservation. *Restoration Ecology*, *29*, e13414.

Lamb, C. T., Ford, A. T., McLellan, B. N., Proctor, M. F., Mowat, G., Ciarniello, L., Nielsen, S. E., & Boutin, S. (2020). The ecology of human–carnivore coexistence. *Proceedings of the National Academy of Sciences*, *117*, 17876–17883.

Lamb, C. T., Roland, W., Carmen, R., Owens-Beek, N., Napoleon, J., Muir, B., McNay, R. S., Lavis, E., Hebblewhite, M., Giguere, L., Dokkie, T., Boutin, S., & Ford, A. T. (2022). Indigenous-led conservation: Pathways to recovery for the nearly extirpated Klinse-Za mountain caribou. *Ecological Applications*, e2581. https://doi.org/10.1002/eap.2581

Latham, A. D. M., Latham, M. C., Mccutchen, N. A., & Boutin, S. (2011). Invading white-tailed deer change wolf–caribou dynamics in northeastern Alberta. *The Journal of Wildlife Management*, *75*, 204–212.

Leclerc, M., Dussault, C., & St-Laurent, M.-H. (2014). Behavioural strategies towards human disturbances explain individual performance in woodland caribou. *Oecologia*, *176*, 297–306.

Leech, H., Jelinski, D. E., DeGroot, L., & Kuzyk, G. (2017). The temporal niche and seasonal differences in predation risk to translocated and resident woodland caribou (*Rangifer tarandus caribou*). *Canadian Journal of Zoology*, *95*, 809–820.

Lesmerises, R., Rebouillat, L., Dussault, C., & St-Laurent, M.-H. (2015). Linking GPS telemetry surveys and scat analyses helps explain variability in black bear foraging strategies. *PLoS One*, *10*, e0129857.

Lewis, K. P., Gullage, S. E., Fifield, D. A., Jennings, D. H., & Mahoney, S. P. (2017). Manipulations of black bear and coyote affect caribou calf survival. *The Journal of Wildlife Management*, *81*, 122–132.

McDevitt-Irwin, J.M., Fuller, S.D., Grant, C., & Baum, J.K. (2015). Missing the safety net: evidence for inconsistent and insufficient management of at-risk marine fishes in Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 1596–1608.

McLaren A. (2016). Wolf Management programs in Northwest Territories, Alaska, Yukon, British Columbia, and Alberta: A review of options for management on the Bathurst Caribou Herd range in the Northwest Territories. File Report 49. Government of Northwest Territories, Yellowknife, Northwest Territories, Canada.

McLellan, M. L., Serrouya, R., McLellan, B. N., Furk, K., Heard, D. C., & Wittmer, H. U. (2012). Implications of body condition on the unsustainable predation rates of endangered mountain caribou. *Oecologia*, *169*, 853–860.

McLoughlin, P. D., Dzus, E., Wynes, B., & Boutin, S. (2003). Declines in populations of woodland caribou. *The Journal of Wildlife Management*, *67*, 755–761.

McNay, R. S., Lamb, C. T., Giguere, L., Williams, S. H., Martin, H., Sutherland, G. D., & Hebblewhite, M. (2022). Demographic responses of nearly extirpated endangered mountain caribou to recovery actions in Central British Columbia. *Ecological Applications*, e2580. https://doi.org/10.1002/eap.2580

Morineau, C., Malcolm, K., Beauchemin, A., & St-Laurent, M.-H. (2022). *Déterminants de la variabilité de productivité des femelles caribous forestiers du secteur La Romaine (Québec, Canada)* (p. 37). Rapport scientifique présenté à Hydro-Québec par l'Université du Québec à Rimouski.

Mosnier, A., Boisjoly, D., Courtois, R., & Ouellet, J.-P. (2008). Extensive predator space use can limit the efficacy of a control program. *The Journal of Wildlife Management*, *72*, 483–491.

Mumma, M. A., Gillingham, M. P., Parker, K. L., Johnson, C. J., & Watters, M. (2018). Predation risk for boreal woodland caribou in human-modified landscapes: Evidence of wolf spatial responses independent of apparent competition. *Biological Conservation*, *228*, 215–223.

Musiani, M., & Paquet, P. C. (2004). The practices of wolf persecution, protection, and restoration in Canada and the United States. *Bioscience*, *54*, 50–60.

Nagy-Reis, M., Dickie, M., Calvert, A. M., Hebblewhite, M., Hervieux, D., Seip, D. R., Gilbert, S. L., Venter, O., DeMars, C., Boutin, S., & Serrouya, R. (2021). Habitat loss accelerates for the endangered woodland caribou in western Canada. *Conservation Science and Practice*, *3*, e437.

Nagy-Reis, M., Dickie, M., Sólymos, P., Gilbert, S. L., DeMars, C. A., Serrouya, R., & Boutin, S. (2020). 'WildLift': An open-source tool to guide decisions for wildlife conservation. *Frontiers in Ecology and Evolution*, *8*, 1–11.

National Research Council. (1997). *Wolves, bears, and their prey in Alaska: Biological and social challenges in wildlife management*. The National Academies Press.

Neufeld, B. T., Superbie, C., Greuel, R. J., Perry, T., Tomchuk, P. A., Fortin, D., & McLoughlin, P. D. (2021). Disturbance-mediated apparent competition decouples in a northern boreal caribou range. *The Journal of Wildlife Management*, *85*, 254–270.

News CBC. (2015, September 17). Pamela Anderson the latest celebrity to call for end to B.C. wolf cull. *CBC News*. https://www.cbc.ca/news/canada/british-columbia/pamela-anderson-calls-on-christy-clark-to-end-b-c-wolf-cull-1.3232711

O'Grady, J. J., Reed, D. H., Brook, B. W., & Frankham, R. (2004). What are the best correlates of predicted extinction risk? *Biological Conservation*, *118*, 513–520.

Ozoga, J. J. (1987). Maximum fecundity in supplementally-fed northern Michigan white-tailed deer. *Journal of Mammalogy*, *68*, 878–879.

Palm, E. C., Fluker, S., Nesbitt, H. K., Jacob, A. L., & Hebblewhite, M. (2020). The long road to protecting critical habitat for species at risk: The case of southern mountain woodland caribou. *Conservation Science and Practice*, *2*, e219.

Parks Canada Agency. (2017). *Multi-species action plan for Jasper National Park of Canada*, Species at Risk Act Action Plan Series (p. 21). Parks Canada Agency.

Peterson, R. O., Woolington, J. D., & Bailey, T. N. (1984). Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs*, *88*, 3–52.

Pinard, V., Dussault, C., Ouellet, J.-P., Fortin, D., & Courtois, R. (2012). Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. *The Journal of Wildlife Management*, *76*, 189–199.

Prior, K. M., Adams, D. C., Klepzig, K. D., & Hulcr, J. (2018). When does invasive species removal lead to ecological recovery? Implications for management success. *Biological Invasions*, *20*, 267–283.

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., & Brashares, J. S. (2009). The rise of the mesopredator. *Bioscience*, *59*, 779–791.

Ray, J. C., Cichowski, D. B., St-Laurent, M.-H., Johnson, C. J., Petersen, S. D., & Thompson, I. D. (2015). Conservation status of caribou in the western mountains of Canada: Protections under the species at risk act, 2002-2014. *Rangifer*, *35*, 49–80.

Ray, J. C., Redford, K. H., Steneck, R., & Berger, J. (2005). *Large carnivores and the conservation of biodiversity*. Island Press.

Rempel, R. S., Carlson, M., Rodgers, A. R., Shuter, J. L., Farrell, C. E., Cairns, D., Stelfox, B., Hunt, L. M., Mackereth, R. W., & Jackson, J. M. (2021). Modeling cumulative effects of climate and development on moose, wolf, and caribou populations. *The Journal of Wildlife Management*, *85*, 1355–1376.

Rettie, W. J., & Messier, F. (1998). Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Canadian Journal of Zoology*, *76*, 251–259.

Roemer, G.W., Donlan, C.J., & Courchamp, F. (2001). Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey. *Proceeedings of the National Academy of Sciences*, *99*, 791–796.

Rominger, E. M. (2018). The Gordian knot of mountain lion predation and bighorn sheep. *The Journal of Wildlife Management*, *82*, 19–31.

Rudolph, T. D., Drapeau, P., Imbeau, L., Brodeur, V., Légaré, S., & St-Laurent, M.-H. (2017). Demographic responses of boreal caribou to cumulative disturbances highlight elasticity of range-specific tolerance thresholds. *Biodiversity and Conservation*, *26*, 1179–1198.

Russell, D. E. (2010). *A review of wolf management programs in Alaska, Yukon, British Columbia, Alberta and Northwest Territories* (p. 47). Whitehorse, Yukon, Canada.

Russell, J. C., Jones, H. P., Armstrong, D. P., Courchamp, F., Kappes, P. J., Seddon, P. J., Oppel, S., Rauzon, M. J., Cowan, P. E., Rocamora, G., Genovesi, P., Bonnaud, E., Keitt, B. S., Holmes, N. D., & Tershy, B. R. (2016). Importance of lethal control of invasive predators for Island conservation. *Conservation Biology*, *30*, 670–672.

Sæther, B.-E., & Haagenrud, H. (1983). Life history of the moose (Alces alces): Fecundity rates in relation to age and carcass weight. *Journal of Mammalogy*, *64*, 226–232.

Santomauro, D., Johnson, C. J., & Fondahl, G. (2012). Historical-ecological evaluation of the long-term distribution of woodland caribou and moose in central British Columbia. *Ecosphere*, *3*, art37.

Schaefer, J. A. (2003). Long-term range recession and the persistence of caribou in the Taiga. *Conservation Biology*, *17*, 1435–1439.

Schneider, R. R., Hauer, G., Adamowicz, W. L., & Boutin, S. (2010). Triage for conserving populations of threatened species: The case of woodland caribou in Alberta. *Biological Conservation*, *143*, 1603–1611.

Seip, D. R. (1992). Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology*, *70*, 1494–1503.

Seip, D. R., Johnson, C. J., & Watts, G. S. (2007). Displacement of mountain caribou from winter habitat by snowmobiles. *The Journal of Wildlife Management*, *71*, 1539–1544.

Serrouya, R., McLellan, B. N., Boutin, S., Seip, D. R., & Nielsen, S. E. (2011). Developing a population target for an overabundant ungulate for ecosystem restoration. *Journal of Applied Ecology*, *48*, 935–942.

Serrouya, R., McLellan, B. N., van Oort, H., Mowat, G., & Boutin, S. (2017). Experimental moose reduction lowers wolf density and stops decline of endangered caribou. *PeerJ*, *5*, e3736.

Serrouya, R., Seip, D. R., Hervieux, D., McLellan, B. N., McNay, R. S., Steenweg, R., Heard, D. C., Hebblewhite, M., Gillingham, M., & Boutin, S. (2019). Saving endangered species using adaptive management. *Proceedings of the National Academy of Sciences*, *116*, 6181–6186.

Simberloff, D., Martin, J. L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., & Vilà, M. (2013). Impacts of biological invasions: What's what and the way forward. *Trends in Ecology & Evolution*, *28*, 58–66.

Skoog, R. O. (1968). *Ecology of the caribou (Rangifer tarandus granti) in Alaska*. University of California.

Slagle, K., Bruskotter, J. T., Singh, A. S., & Schmidt, R. H. (2017). Attitudes toward predator control in the United States: 1995 and 2014. *Journal of Mammalogy*, *98*, 7–16.

Spalding, D. J. (2000). *The early history of woodland caribou (Rangifer tarandus caribou) in British Columbia*. B-100, Wildlife Bulletin (p. 61). BC Ministry of Environment, Lands and Parks. https://www.sciencebase.gov/catalog/item/572a2a58e4b0b13d391a06f4

St-Laurent, M.-H., & Dussault, C. (2012). The reintroduction of boreal caribou as a conservation strategy: A long-term assessment at the southern range limit. *Rangifer*, *32*, 127–138.

Treves, A., Krofel, M., Ohrens, O., & van Eeden, L. M. (2019). Predator control needs a standard of unbiased randomized experiments with cross-over design. *Frontiers in Ecology and Evolution*, *7*, 462.

Valkenburg, P., McNay, M. E., & Dale, B. W. (2004). Calf mortality and population growth in the Delta caribou herd after wolf control. *Wildlife Society Bulletin*, *1973-2006*(32), 746–756.

Wallach, A. D., Bekoff, M., Nelson, M. P., & Ramp, D. (2015). Promoting predators and compassionate conservation. *Conservation Biology*, *29*, 1481–1484.

Wasser, S. K., Keim, J. L., Taper, M. L., & Lele, S. R. (2011). The influences of wolf predation, habitat loss, and human activity on caribou and moose in the Alberta oil sands. *Frontiers in Ecology and the Environment*, *9*, 546–551.

Webb, N. F., Allen, J. R., & Merrill, E. H. (2011). Demography of a harvested population of wolves (*Canis lupus*) in west-central Alberta, Canada. *Canadian Journal of Zoology*, *89*, 744–752.

Wittmer, H. U., Sinclair, A. R. E., & McLellan, B. N. (2005). The role of predation in the decline and extirpation of woodland caribou. *Oecologia*, *144*, 257–267.

Wolf, C., & Ripple, W. J. (2017). Range contractions of the world's large carnivores. *Royal Society Open Science*, *4*, 170052.

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